Posted on 22 Nov 2024 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.173226964.47195579/v1 — This is a preprint and has not been peer-reviewed. Data may be preliminary.

Unraveling dynamic omnivory and community interactions between primary producers and an apex predator

Ashlee Mikkelsen[1], Andreas Zedrosser[2], Agnieszka Sergiel[3], Keith Hobson[4], Nuria Selva[5], and Anne Hertel[6]

[1]University of South-Eastern Norway
[2]University College of Southeast Norway
[3]Institute of Nature Conservation Polish Academy of Sciences
[4]Western University
[5]Polish Academy of Sciences
[6]Universitet for Miljo- og Biovitenskap Naturforvaltning INA

November 22, 2024

Abstract

The effects of climate and plant phenological changes on herbivorous species are widely recognized, yet less research has focused on omnivorous and carnivorous species, even though they also have vegetative components to their diet. The historical focus on predators regarding simple interactions between obligate carnivores and their prey over-simplifies many species' roles within ecological communities by casting them purely as predators and minimizes other, equally important roles within the community. We used a long-term, individual-based data set on a polyphagous mammal, the brown bear (Ursus arctos), to estimate diet over 25 years identify long-term patterns and factors contributing to annual variation in diet. We used carbon and nitrogen stable isotope values measured in hair and Bayesian mixing models to determine annual diet among three demographic bear classes, and then used linear regression models to relate diet to indices of food availability. We found that while diet varied among years and demographic classes, variation in both carbon and nitrogen values were explained by bilberry (Vaccinium myrtillus) productivity. Additionally, proportions of animal-derived foods decreased through time, while proportions of bilberry increased, even as the moose population in Sweden increased over this same period. While meat and animal-derived foods are considered higher quality foods for bears, bear diet did not respond to changing moose availability. Our results highlight that even though vegetative diet components in predators are typically considered less important to predator ecology, brown bears in Sweden responded to changes in primary production, regardless of prey availability. It will be crucial to put more emphasis on the vegetative parts of diets as we predict how species and ecological communities respond to climate change because predators serve many more functions within their community besides predation alone.

TITLE: Unraveling dynamic omnivory and community interactions between primary producers and an apex predator

ABSTRACT

The effects of climate and plant phenological changes on herbivorous species are widely recognized, yet less research has focused on omnivorous and carnivorous species, even though they also have vegetative components to their diet. The historical focus on predators regarding simple interactions between obligate carnivores and their prey over-simplifies many species' roles within ecological communities by casting them purely as predators and minimizes other, equally important roles within the community. We used a long-term, individual-based data set on a polyphagous mammal, the brown bear (*Ursus arctos*), to estimate diet over 25 years identify long-term patterns and factors contributing to annual variation in diet. We used

Posted on 22 Nov 2024 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.173226964.47195579/v1 — This is a preprint and has not been peer-reviewed. Data may be preliminary.

carbon and nitrogen stable isotope values measured in hair and Bayesian mixing models to determine annual diet among three demographic bear classes, and then used linear regression models to relate diet to indices of food availability. We found that while diet varied among years and demographic classes, variation in both carbon and nitrogen values were explained by bilberry (*Vaccinium myrtillus*) productivity. Additionally, proportions of animal-derived foods decreased through time, while proportions of bilberry increased, even as the moose population in Sweden increased over this same period. While meat and animal-derived foods are considered higher quality foods for bears, bear diet did not respond to changing moose availability. Our results highlight that even though vegetative diet components in predators are typically considered less important to predator ecology, brown bears in Sweden responded to changes in primary production, regardless of prey availability. It will be crucial to put more emphasis on the vegetative parts of diets as we predict how species and ecological communities respond to climate change because predators serve many more functions within their community besides predation alone.

Keywords: brown bear, carnivore, diet, omnivory, primary productivity, stable isotopes, *Ursus arctos* , *Vaccinium* .

1 | INTRODUCTION

Some terms in ecology hold specific connotations, that when used, can limit our perceptions about ecological processes, bias our results, and hinder our understanding of the natural world. For instance, the term “carnivore” can be confusing in ecology, either referring specifically to members of the mammalian order Carnivora, or more generally referring to animals (typically mammals) that kill and consume other vertebrates (i.e., meat-eaters; Gittleman, 2013; Yoshimura et al., 2021). However, outside a few families of obligate carnivores (felids and hyenids; Clauss et al., 2010; Yoshimura et al., 2021), members of Carnivora eat a wide variety of foods, including invertebrates, plants and fungi (Edwards et al., 2011). Additionally, many species in groups outside Carnivora, such as primates, rodents, raptors, reptiles, amphibians, fish, invertebrates, and plants (Román-Palacios et al., 2019), kill and consume vertebrates. Thus, classic foraging categories of carnivore, omnivore, and herbivore may be overly simplistic (Harrer & Levi, 2018; Leigh et al., 2018; Vazquez et al., 2023) and lead to a narrow focus on an organism’s diet. Using a more precise term, such as polyphagous (Loxdale & Harvey, 2023), may combat this issue.

Food webs have traditionally modelled polyphagous species as static consumers exerting constant pressure on multiple resources, but diet specificity changes with environmental conditions and is essential to ecosystem stability (Gutgesell et al., 2022). Primary productivity varies annually related to climate and insect or pathogen abundance (Bjerke et al., 2014) and organisms can respond to this variation by changing their diet. Thus, polyphagous species can rapidly respond to changes in resource availability (Deacy et al., 2018), relieving pressure from an exhausted resource while increasing pressure on another, more abundant resource, even if the second resource is a less-preferred food (Zhang et al., 2021). The historical focus on predators through simple interactions between large, charismatic, obligate carnivores and their prey over-simplifies many polyphagous species’ roles within ecological communities (Miller et al., 2001). This likely overlooks trophic interactions which may be important to community stability (Kratina et al., 2012) and essential to predict community shifts in a changing climate (Gutgesell et al., 2022).

Despite the need for a deeper understanding of polyphagous species beyond their roles as predators, measuring diet in wild species is difficult (Davis & Pineda-Munoz, 2016) and modeling environmental features associated with diet changes is challenging due to the complexity of ecological communities. One way to estimate diet in wildlife is through stable isotope analysis (Tieszen & Boutton, 1989). This method is based on the principal that the ratio of naturally occurring stable isotopes varies across the earth and among different food types, such as C-4 and C-3 plants or marine and terrestrial animals, and all organisms must build their tissues from molecules they consume (Tieszen & Boutton, 1989). Thus, the stable isotope value of an organisms’ tissue will most closely resemble that of its dominant foods (Semmens et al., 2009).

In addition to diet estimation, accurate measures of food availability are difficult to obtain, especially over time periods long enough to detect change (Davis & Pineda-Munoz, 2016). Even within the same population of a single species, there will be differences in diet among individuals (Edwards et al., 2011), demographic classes (Beck et al., 2007), across space (Stern et al., 2024), and time (Davis & Pineda-Munoz, 2016), which can obscure general patterns. For example, within a species different populations may have different responses to variation in primary productivity, such as mast crops (Hertel et al., 2019; Schwartz et al., 2010). Thus, determining the effect of variation in primary productivity on diet of polyphagous species is challenging.

We used a dataset on a polyphagous mammal, the brown bear (*Ursus arctos*), to estimate annual diet proportions of common foods as well as identify diet patterns and drivers over 25 years. We used carbon (δ ^{13}C) and nitrogen (δ ^{15}N) stable isotopes measured in hair of known individual bears in south-central Sweden to estimate annual diet among different demographic classes. We focused on the five primary diet components of bears in this system: ants (*Formnica* spp. and *Camponotus* spp.), bilberry (*Vaccinium myrtillus*), crowberry *(Empetrum nigrum),* lingonberry*(Vaccinium vitus-vitae),* and moose *(Alces alces* ; Stenset et al., 2016). Berry production in Scandinavia is variable both temporally and spatially (Hertel et al., 2016), while moose populations showed less variation (Jensen et al., 2020). Based on previous stable isotope analyses (Mikkelsen et al., 2023), we expected bilberry to make up the greatest proportion of the brown bear diet, however meat is considered higher quality food than berries (Pritchard & Robbins, 1990). Thus, while it accounts for a smaller diet proportion, we expected brown bear diet to respond to moose availability (Hypothesis 1); years with greater numbers of moose will be associated with greater proportions of moose in the diet. Moose populations have been increasing across Scandinavia (Jensen et al., 2020), and proportions of moose in the diet should increase through time as bears respond to increasing moose availability (Hypothesis 2). Annual variation in food productivity will also result in annual variation in stable isotope values. Specifically, we expected δ ^{15}N values to be related to indices of moose population size andδ ^{13}C values to be related to annual bilberry production (Hypothesis 3).

2 | METHODS

2.1 | Study system

Our study area encompassed ˜13,000 km^{2}in Gävleborg and Dalarna counties in southcentral Sweden with low human density and heavily managed forests of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Bears were captured via remote drug delivery from a helicopter (Arnemo & Evans, 2017) in spring soon after den emergence (March–May). All capture procedures were conducted in accordance with the Swedish Environmental Protection Agency, Swedish Board of Agriculture, and Swedish Ethical Committee on Animal Research.

2.2 | Sample collection

Bear hair samples were collected from between the shoulders of brown bears during spring captures 1995–2020. After collection, hair samples were placed in individual paper envelopes, labeled accordingly and stored dry at room temperature. To estimate brown bear diet proportions, we also collected brown bear foods within the study area in 2014 and 2015. We collected hair from between the shoulder blades of local, wild moose harvested during the regular hunting season in 2014. Because the moose harvest in Sweden includes all demographic classes of the population, our moose hair sample set includes adults and sub-adults of both sexes. Wild berries (fruits) of the three primary species consumed (bilberry, lingonberry and crowberry) were collected from random locations within the study area in summer 2014. Ants of the genera*Formica* and *Camponotus* were also collected within the study area in the summer of 2014. Specimens were mostly adult workers collected from ant hills (*Camponotus*) and by sampling coarse woody debris and tree stumps (*Formica*) in clearcuts of different age classes at random locations in the study area.

2.3 | Stable isotope analysis

When processing brown bear hair, we separated as much underfur as possible out of the sample, removed large surface contaminants, and weighed hairs to the nearest milligram. Preparatory procedures followed the protocol for cortisol concentration measurement (Macbeth et al., 2010) and samples for stable isotope

Posted on 22 Nov 2024 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.173226964.47195579/v1 — This is a preprint and has not been peer-reviewed. Data may be preliminary.

Posted on 22 Nov 2024 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.173226964.47195579/v1 — This is a preprint and has not been peer-reviewed. Data may be preliminary.

estimation were portioned out after the grinding step (Sergiel et al., 2017; Appendix S2). We washed each sample three times with 40 µl HPLC grade methanol per mg hair for three minutes per wash to remove other external contaminants (Sergiel et al., 2020). After the hair had dried for at least 24 hours, it was ground to a fine powder in a mixer mill (Retsch MM4000; Retsch GmbH, Germany) at 30 Hz and then put into plastic vials. To measure$\delta\,^{13}$C and $\delta\,^{15}$N in hair, we followed Koehler at al. (2019) and weighed 1 mg of powdered hair into precombusted tin capsules. Encapsulated hair was combusted at 1030°C in a Carlo Erba NA1500 or Eurovector 3000 elemental analyser. The resulting N_2 and CO_2 were separated chromatographically and introduced to an Elementar Isoprime or a Nu Instruments Horizon isotope ratio mass spectrometer. We used two reference materials to normalize the results to VPDB and AIR: BWBIII keratin ($\delta\,^{13}$C = -20.18,$\delta\,^{15}$N = +14.31 per mil, respectively) and PRCgel ($\delta\,^{13}$C = -13.64, $\delta\,^{15}$N= +5.07 per mil, respectively). Within run (n = 5) precisions as determined from both reference and sample duplicate analyses and from QA/QC controls were ± 0.1 per mil for both $\delta\,^{13}$C and $\delta\,^{15}$N.

We corrected $\delta\,^{13}$C values for the anthropogenic depletion of ^{13}C in the atmosphere (i.e., the Suess Effect) by applying a -0.0222005) and used results from published feeding experiments on ursids (Felicetti et al., 2003; Hilderbrand et al., 1996; Rode et al., 2016) to estimate the isotopic discrimination factors (TDFs) between bear hair and bear serum (Appendix S1.a). We used a similar procedure to estimate TDFs between moose hair and moose meat and offal (Appendix S1.b).

2.4 | Statistical analysis

To answer our hypotheses stated above, we did two separate analyses. First, we used stable isotopes and Bayesian mixing models to estimate annual dietary proportions among three different demographic classes to estimate annual diet over the 25-year study period. Second, we used linear regression models to explain annual variation in dietary proportions and stable isotopes relative to indices of annual food availability.

2.4.1 | Dietary proportion estimation

Based on previous research, we expected brown bear dietary proportions to vary among the demographic classes of independent (no longer dependent on their mother) bears in our population (Steyaert et al., 2013; Swenson et al., 2007).We subset the stable isotope data by demographic classes (females with dependent offspring, solitary females, and solitary males) and ran three separate diet estimation models using year and bearID as random effects. We used previous diet estimates for our population (Mikkelsen et al., 2023) to derive informative priors for our models. We removed six outliers that had particularly high$\delta\,^{13}$C values and fell outside the mixing polygon. Each model was run with three chains with 3000000 iterations, a burn-in of 1500000 and a thin rate of 500. We used graphical output as well as fit statistics to determine if each model had run for sufficient time to converge and to ensure proper chain mixing (Semmens et al., 2009; Stock et al., 2018). All analysis was completed in R (R Core Team, 2024) using package MixSIAR (Stock & Semmens, 2013).

Model estimates of the dietary proportions of moose in males had a distinct bimodal distribution, which may arise from the model failing to converge on a single estimate, or from the population having two different diets among males in our sample (i.e., two different possible solutions to the equation). Larger, older males may be more predatory than younger bears (Welch *et al* ., 1997), thus the bimodal distribution may represent the proportion of moose in the diet for subadult males vs. adult males. To test this, we included an additional*a posteriori* model for males with an adult and subadult categorical variable as a fixed effect to determine whether this resolved the bimodal distribution.

2.4.2 | Annual variability in food availability

Berries. We used berry inventory information from the Siljansfors Experimental Forest, which is adjacent to the bear monitoring area to estimate the annual productivity of bilberry and lingonberry. Each year, berry production on 54-60 0.25 m^2 circular plots was inventoried 2006– 2020. The number of ripe bilberries were counted between July and end of August and the number of ripe lingonberries were counted between end of August and mid-September. Following Hertel et al. (2018), we calculated an annual berry production

Posted on 22 Nov 2024 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.173226964.47195579/v1 — This is a preprint and has not been peer-reviewed. Data may be preliminary.

index as the annual deviation of berry abundance from the 14-year average for each plot. We then created a model to predict berry production with year as a fixed effect and predicted the annual deviation of berries produced. This was scaled between 0 and 1 with indices approaching 0 denoting years of lower-than-average berry production and indices approaching 1 denoting years of higher-than-average berry production (Hertel et al., 2018).

Moose. Moose harvest and observation data was downloaded from Statistik älgdata (https://algdata-apps.lansstyrelsen.se/algdata-apps-stat; Singh et al., 2014) for the counties of Gävleborg and Dalarna. Data in this system are citizen-reported moose observations in the first seven days of the hunting season (October) adjusted by observer effort/observation hours. In Sweden, reporting harvested moose is required by law (Singh et al., 2014). The moose observation database also records the sex, age (calves and adults) and the number of calves with an observed female (singles vs twins), which indicates the overall moose population size, as well as the annual recruitment rate of calves surviving from birth in spring to the fall (Kalén et al., 2022). We used the annual number of total moose observed and harvested after accounting for hunter effort (Singh et al., 2014) as indicator of moose population size. We also used the total number of calves observed as an indicator of annual calf production because calves represent the age class most commonly preyed on by bears in the study area (Swenson et al, 2007).

2.4.3 | Linear regression modelling and model selection

We used mixed-effects linear regression models with the lme4 package (Bates et al., 2014) in R (R Core Team, 2024) to explain variation in diet proportions, δ^{13}C, andδ^{15}N values within our population based on*a priori* hypotheses (Table S1). We used individual ID and demographic class (females with dependent offspring, solitary males, and solitary females) as random effects and used a build-up modeling strategy in which we began by determining the best relationship for each covariate considered (linear, log-linear, or quadratic), and then retained that structure throughout modelling. We used bear age, sex, and annual indices of food availability as fixed effects. All models were compared to the null model to determine whether fixed effects explained more variation than the intercept only, and variables that performed better than the intercept only were used to build more complex models that included additive effects and two-way interactions. We used an information-theoretic criterion for small sample sizes (AIC$_c$) and the relative differences between models (ΔAIC$_c$) when determining the model with the best fit given the data for final inferences (Burnham & Anderson, 2002). For models with similar AIC$_c$ values, we compared beta estimates, the 95% confidence intervals around the beta estimates, and model variance to select the most parsimonious model (Burnham & Anderson, 2002).

Although we had bear data from 1995–2020, our annual food availability data was limited to 2006–2020, restricting our inference regarding the drivers of variation in δ^{13}C andδ^{15}N to this 14-year period. Prior to analysis, we compared the demographic composition, means, medians, and standard errors of our subset data (2006–2020) to the full dataset (1995–2020) to ensure there were no obvious differences in the data (Supplementary Materials S3).

Diet proportions were estimated using the full data set and each demographic class separately, and we used the subset data (2006–2020) and all demographic classes together for linear regression modelling explaining variation in diet proportion and stable isotope values.

3 | RESULTS

To estimate annual diet proportions, we had 190 records from 71 females with dependent offspring (aged 4–24), 239 records from 118 solitary females (aged 1–21), and 257 records from 83 solitary males (aged 1–29). Despite the isotopic similarities between two berry species (lingonberry and crowberry) as well as ants and moose, the model produced good estimates for these foods (Supplementary Materials S2, Figure S3).

For the linear regression analysis explaining variation in diet proportions and isotope values, we had 669 records of 268 bears (aged 2–19) representing 1995–2020. The subset data including annual bilberry production indices 2006–2020 consisted of 410 records of 177 bears (aged 2–19).

Posted on 22 Nov 2024 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.173226964.47195579/v1 — This is a preprint and has not been peer-reviewed. Data may be preliminary.

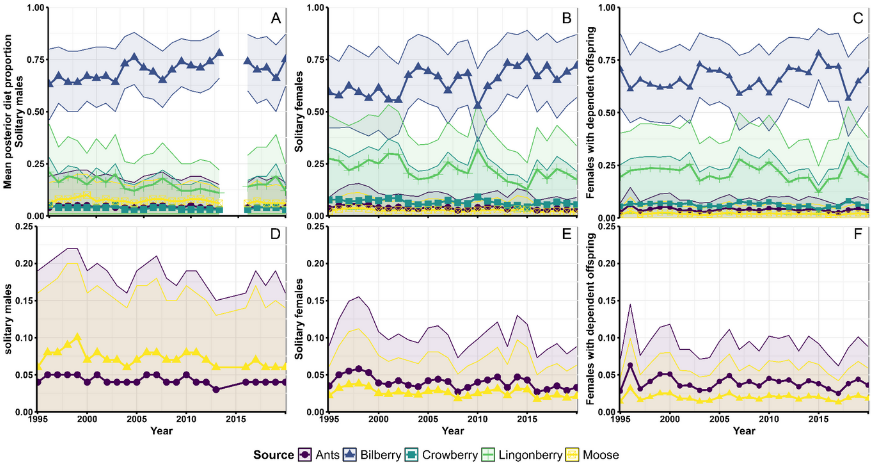


Figure 1. Annual mean estimates of diet proportions for three demographic classes of brown bears in Sweden: solitary males (A & D), solitary females (B & E), and females with dependent offspring (C & F). Males are included as one demographic class rather than by age group (subadult vs adult) because sample sizes prevented us from looking at changes in male diet proportions between the two age classes. Panels A-C show proportions of all 5 food sources, whereas panels D-F only include protein rich foods (moose and ants)

Ants and moose were consumed in similar proportions across years (Figure 1 D-E) and there was evidence that the proportion of ants and moose decreased over time ($\widehat{\beta}_{(\text{Ants.Year})} = -0.04,\ SE = 0.004$; $\widehat{\beta}_{(\text{Moose.Year})} = -0.02,\ SE = 0.002$), while the proportion of bilberry in the diet remained stable or slightly increased over time ($\widehat{\beta}_{(\text{Bilberry.Year})} = 0.01,\ SE = 0.005$; Table S1). The beta estimates translate to very small changes in diet, with ants and moose proportions decreasing by a 0.25 and 0.025 of 1% each year, respectively. Meanwhile bilberry increased by 0.01 of 1% each year. Over the 25-year study, for solitary female bears, the estimated mean proportions of ants declined from 4.2% to 3.3%, moose declined from 3.9% to 2.9% and estimated mean proportions of bilberry increased from 52% to 55%.

3.2 | Patterns in stable isotope values

There was annual variation in $\delta\,^{13}$C values (Figure 2A), and this variation was best described by a log-linear relationship with bilberry production and the number of moose calves observed in the year in which hair was grown (Table 1). Higher$\delta\,^{13}$C values are associated with moose and ants, median values are associated with crowberry and lingonberry, and bilberry had the lowest $\delta\,^{13}$C values.

Posted on 22 Nov 2024 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.173226964.47195579/v1 — This is a preprint and has not been peer-reviewed. Data may be preliminary.

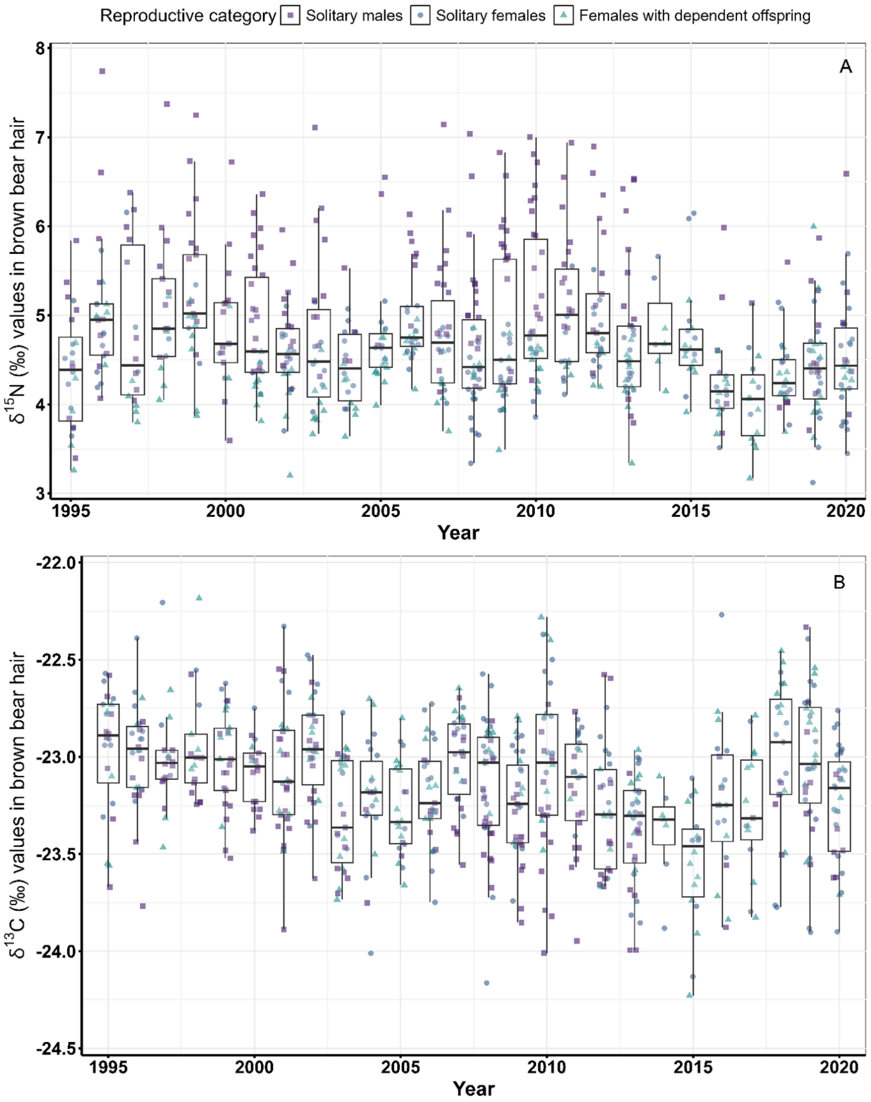


Figure 2**.** Annual variation in hair stable isotope values for nitrogen ($\delta\ ^{15}$N, A) and carbon ($\delta\ ^{13}$C, B) for a population of brown bears in Sweden 199–2020. Box plots depict the annual means, quantiles, and outliers, while colored points depict the observed values by demographic class.

There was strong support in the data that $\delta\ ^{13}$C values were lower in years with greater bilberry production ($\widehat{\beta}_{(\ln(\text{Bilberry}))} = -0.21,\ 95\%\ CI = -0.30\ to - 0.12$) and greater numbers of observed moose calves ($\widehat{\beta}_{(\text{MooseCalves})} = \ -0.25,\ 95\%\ CI = -0.35\ to - 0.14$). animal foods (i.e., moose and ants) had the highest$\delta\ ^{13}$C values, crowberry and lingonberry had median $\delta\ ^{13}$C values, and bilberry had the lowest$\delta\ ^{13}$C value. In years with high bilberry production, brown bear $\delta\ ^{13}$C values were more similar to bilberry, which should indicate a diet higher in bilberry, even when moose calf numbers were high.

Posted on 22 Nov 2024 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.173226964.47195579/v1 — This is a preprint and has not been peer-reviewed. Data may be preliminary.

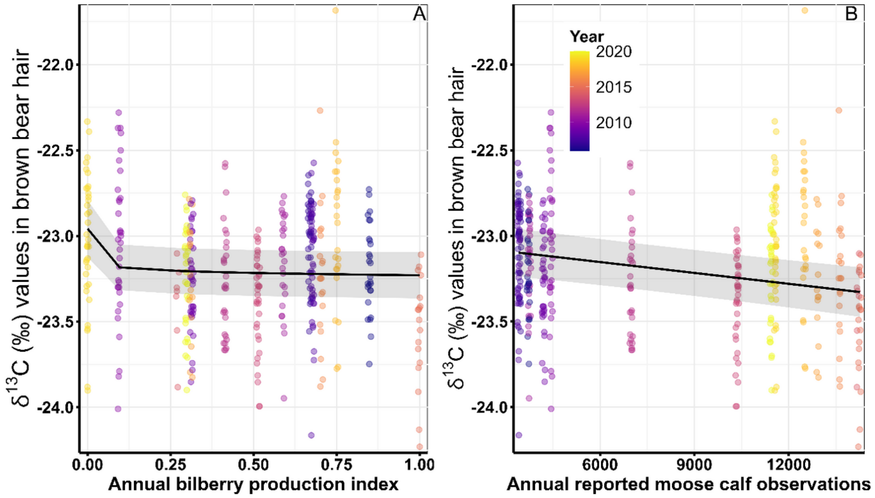
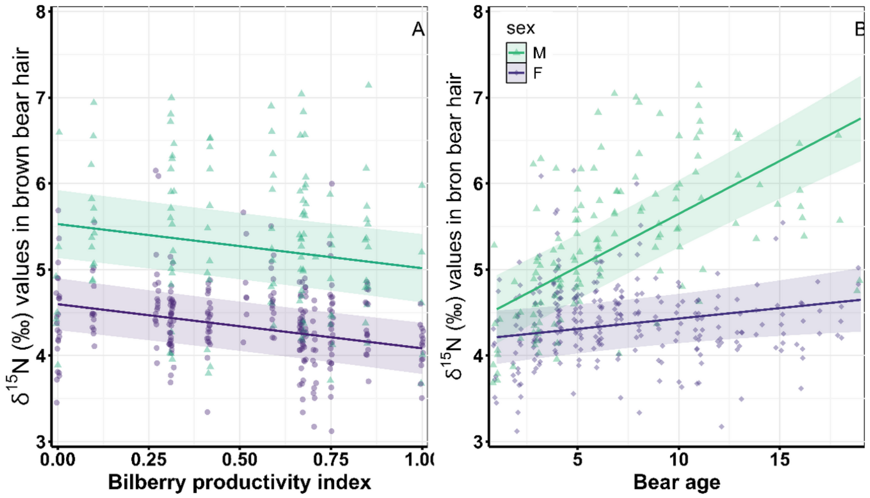


Figure 3. Fitted relationships between $\delta\,^{13}$C measured in brown bear hair collected in Southcentral Sweden 2006–2020 and the annual number of estimated moose calves from hunter observations after accounting for observer effort (3A) and the annual index of bilberry production (3B). Lines are the fitted relationships from the top model with 95% confidence intervals shaded around the lines. Colored points represent the raw data collected, with darker colors representing earlier years and lighter colors representing later years.

$\delta\,^{15}$N values varied annually (Figure 2B) and was best described by the annual proportion of moose in the diet, but$\delta\,^{15}$N values were not correlated with indices of moose availability. Instead, variation in $\delta\,^{15}$N was best explained by the bilberry production index with a one-year time lag (berry production in *t* affecting stable isotope values in*t+1* : Table 1, Figure 4A) while accounting for sex-specific age (Figure 4B).



5 | LITERATURE CITED

Arnemo, J. M., & Evans, A. L. (2017). Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx. Innland Norway University of Applied Sciences, January, 1–18.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* , **67** . https://doi.org/10.18637/jss.v067.i01

Posted on 22 Nov 2024 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.173226964.47195579/v1 — This is a preprint and has not been peer-reviewed. Data may be preliminary.

Beck, C., Rea, L., Iverson, S., Kennish, J., Pitcher, K., & Fadely, B. (2007). Blubber fatty acid profiles reveal regional, seasonal, age-class and sex differences in the diet of young Steller sea lions in Alaska. *Marine Ecology Progress Series* , **338** , 269–280. https://doi.org/10.3354/meps338269

Bjerke, J. W., Rune Karlsen, S., Arild Høgda, K., Malnes, E., Jepsen, J. U., Lovibond, S., Vikhamar-Schuler, D., & Tømmervik, H. (2014). Record-low primary productivity and high plant damage in the Nordic Arctic Region in 2012 caused by multiple weather events and pest outbreaks.*Environmental Research Letters* , **9** , 084006. https://doi.org/10.1088/1748-9326/9/8/084006

Borchert, M., & Tyler, C. M. (2011). Desiccation sensitivity and heat tolerance of *Prunus ilicifolia* seeds dispersed by American black bears (*Ursus americanus*). *Western North American Naturalist* , **70** , 457–466. https://doi.org/10.3398/064.070.0405

Burnham, K. P., & Anderson, D. R. (2002). Model Selection and Inference: A Practical Information-Theoretic Approach. In *The Journal of Wildlife Management* (Second). https://doi.org/10.2307/3803117

Chamberlain, C. P., Waldbauer, J. R., Fox-Dobbs, K., Newsome, S. D., Koch, P. L., Smiths, D. R., & Church, M. E. (2005). Pleistocene to recent dietary shifts in California condors. *Proceedings of the National Academy of Sciences of the United States of America* , **102** , 16707–16711. https://doi.org/10.1073/pnas.0508529102

Clauss, M., Kleffner, H., & Kienzle, E. (2010). Carnivorous mammals: Nutrient digestibility and energy evaluation.*Zoo Biology* , **29** , 687–704. https://doi.org/10.1002/zoo.20302

Davis, M., & Pineda-Munoz, S. (2016). The temporal scale of diet and dietary proxies. *Ecology and Evolution* , **6** , 1883–1897. https://doi.org/10.1002/ece3.2054

Deacy, W. W., Armstrong, J. B., Leacock, W. B., Robbins, C. T., Gustine, D. D., Ward, E. J., Erlenbach, J. A., & Stanford, J. A. (2017). Phenological synchronization disrupts trophic interactions between Kodiak brown bears and salmon. *Proceedings of the National Academy of Sciences of the United States of America* , **114,** 10432–10437. https://doi.org/10.1073/pnas.1705248114

Edwards, M. A., Derocher, A. E., Hobson, K. A., Branigan, M., & Nagy, J. A. (2011). Fast carnivores and slow herbivores: Differential foraging strategies among grizzly bears in the Canadian Arctic. *Oecologia* , **165** , 877–889. https://doi.org/10.1007/s00442-010-1869-9

Farley, S. D., & Robbins, C. T. (1995). Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Canadian Journal of Zoology* , **73** , 2216–2222. https://doi.org/10.1139/z95-262

Felicetti, L. A., Schwartz, C. C., Rye, R. O., Haroldson, M. A., Gunther, K. A., Phillips, D. L., & Robbins, C. T. (2003). Use of sulfur and nitrogen stable isotopes to determine the importance of whitebark pine nuts to Yellowstone grizzly bears. *Canadian Journal of Zoology* ,**81** , 763–770. https://doi.org/10.1139/z03-054

Gallinat, A. S., Primack, R. B., & Wagner, D. L. (2015). Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution* , **30** , 169–176. https://doi.org/10.1016/j.tree.2015.01.004

Garcia-Rodriguez, A., Selva, N., Zwijacz-Kozica, T., Albrecht, J., Lionnet, C., Rioux, D., Taberlet, P., & De Barba, M. (2021). The bear-berry connection: Ecological and management implications of brown bears' food habits in a highly touristic protected area. Biological Conservation, 264. https://doi.org/10.1016/j.biocon.2021.109376

Gittleman, J. L. (2013). Carnivore Behavior, Ecology, and Evolution. In J. L. Gittleman (Ed.), Carnivore Behavior, Ecology, and Evolution. Springer US. https://doi.org/10.1007/978-1-4757-4716-4

Gutgesell, M. K., McCann, K. S., Gellner, G., Cazelles, K., Greyson-Gaito, C. J., Bieg, C., Guzzo, M. M., Warne, C. P. K., Ward, C. A., O'Connor, R. F., Scott, A. M., Graham, B. C., Champagne, E. J., & McMeans, B. C. (2022). On the dynamic nature of omnivory in a changing world. *BioScience,* **72** , 416–430. https://doi.org/10.1093/biosci/biab144

Harrer, L. E. F., & Levi, T. (2018). The primacy of bears as seed dispersers in salmon-bearing ecosystems.*Ecosphere,* **9** . https://doi.org/10.1002/ecs2.2076

Hertel, A. G., Bischof, R., Langval, O., Mysterud, A., Kindberg, J., Swenson, J. E., & Zedrosser, A. (2018). Berry production drives bottom-up effects on body mass and reproductive success in an omnivore. *Oikos* , **127** , 197–207. https://doi.org/10.1111/oik.04515

Hertel, A. G., Steyaert, S. M. J. G., Zedrosser, A., Mysterud, A., Lodberg-Holm, H. K., Gelink, H. W., Kindberg, J., & Swenson, J. E. (2016). Bears and berries: species-specific selective foraging on a patchily distributed food resource in a human-altered landscape. Behavioral Ecology and Sociobiology, 70(6), 831–842. https://doi.org/10.1007/s00265-016-2106-2

Hertel, A. G., Zedrosser, A., Kindberg, J., Langvall, O., & Swenson, J. E. (2019). Fluctuating mast production does not drive Scandinavian brown bear behavior. *Journal of Wildlife Management* , **83** 657–668. https://doi.org/10.1002/jwmg.21619

Hilderbrand, G. V., Farley, S. D., Robbins, C. T., Hanley, T. A., Titus, K., & Servheen, C. (1996). Use of stable isotopes to determine diets of living and extinct bears. *Canadian Journal of Zoology* , **74** , 2080–2088. https://doi.org/10.1139/z96-236

Homkes, A. T., Gable, T. D., Windels, S. K., & Bump, J. K. (2020). Berry important? Wolf provisions pups with berries in Northern Minnesota. *Wildlife Society Bulletin* , **44** , 221–223. https://doi.org/10.1002/wsb.1065

Kalen, C., Andren, H., Mansson, J., & Sand, H. (2022). Using citizen data in a population model to estimate population size of moose (*Alces alces*). *Ecological Modelling* , **471** . https://doi.org/10.1016/j.ecolmodel.2022.110066

Koehler, G., Kardynal, K. J., & Hobson, K. A. (2019). Geographical assignment of polar bears using multi-element isoscapes. *Scientific Reports* , **9** , 9390. https://doi.org/10.1038/s41598-019-45874-w

Kratina, P., LeCraw, R. M., Ingram, T., & Anholt, B. R. (2012). Stability and persistence of food webs with omnivory: Is there a general pattern? *Ecosphere* ,**3,** art50. https://doi.org/10.1890/es12-00121.1

Leigh, S. C., Papastamatiou, Y. P., & German, D. P. (2018). Seagrass digestion by a notorious 'carnivore.' *Proceedings of the Royal Society B: Biological Sciences* , **285** . https://doi.org/http://dx.doi.org/10.1098/rspb.2018.1583

Loxdale, H. D., & Harvey, J. A. (2023). Generalism in nature: A community ecology perspective. *Community Ecology* ,**24** , 113–125. https://doi.org/10.1007/s42974-022-00130-6

Macbeth, B. J., Cattet, M. R. L., Stenhouse, G. B., Gibeau, M. L., & Janz, D. M. (2010). Hair cortisol concentration as a noninvasive measure of long-term stress in free-ranging grizzly bears (*Ursus arctos*): Considerations with implications for other wildlife. *Canadian Journal of Zoology* , **88** , 935–949. https://doi.org/10.1139/Z10-057

Mikkelsen, A. J., Hobson, K. A., Sergiel, A., Hertel, A. G., Selva, N., & Zedrosser, A. (2023). Testing foraging optimization models in brown bears: Time for a paradigm shift in nutritional ecology? *Ecology,* **105** . https://doi.org/10.1002/ecy.4228

Miller, B., Dugelby, B., Foreman, D., Martinez, C., Rio, D., Phillips, M., Reading, R., Soule, M. E., Terborgh, J., & Willcox, L. (2001). The importance of large carnivores to healthy ecosystems. *Endangered Species,* **18,** 202–210.

Orsenigo, S., Mondoni, A., Rossi, G., & Abeli, T. (2014). Some like it hot and some like it cold, but not too much: Plant responses to climate extremes. *Plant Ecology* , **215** , 677–688. https://doi.org/10.1007/s11258-014-0363-6

Posted on 22 Nov 2024 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.173226964.47195579/v1 — This is a preprint and has not been peer-reviewed. Data may be preliminary.

Posted on 22 Nov 2024 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.173226964.47195579/v1 — This is a preprint and has not been peer-reviewed. Data may be preliminary.

Pirotta, E., Thomas, L., Costa, D. P., Hall, A. J., Harris, C. M., Harwood, J., Kraus, S. D., Miller, P. J. O., Moore, M. J., Photopoulou, T., Rolland, R. M., Schwacke, L., Simmons, S. E., Southall, B. L., & Tyack, P. L. (2022). Understanding the combined effects of multiple stressors: A new perspective on a longstanding challenge. *Science of the Total Environment,* **82.** https://doi.org/10.1016/j.scitotenv.2022.153322

Platt, S. G., Elsey, R. M., Liu, H., Rainwater, T. R., Nifong, J. C., Rosenblatt, A. E., Heithaus, M. R., & Mazzotti, F. J. (2013). Frugivory and seed dispersal by crocodilians: An overlooked form of saurochory? *Journal of Zoology* , **291** , 87–99. https://doi.org/10.1111/jzo.12052

Plos, C., Hensen, I., Korell, L., Auge, H., & Romermann, C. (2024). Plant species phenology differs between climate and land-use scenarios and relates to plant functional traits. *Ecology and Evolution* , **14** . https://doi.org/10.1002/ece3.11441

Pritchard, G. T., & Robbins, C. T. (1990). Digestive and metabolic efficiencies of grizzly and black bears. *Canadian Journal of Zoology* , **68** , 1645–1651. https://doi.org/10.1139/z90-244

R Core Team. (2024). A language and environment for statistical computing. R Foundation for Statistical Computing. Https://Www.R-Project.Org/. http://www.r-project.org/

Reimchen, T. E. (2017). Diverse ecological pathways of salmon nutrients through an intact marine-terrestrial interface. *Canadian Field-Naturalist* , **131,** 350–368. https://doi.org/10.22621/cfn.v131i4.1965

Robbins, C. T., Christian, A. L., Vineyard, T. G., Thompson, D., Knott, K. K., Tollefson, T. N., Fidgett, A. L., & Wickersham, T. A. (2022). Ursids evolved early and continuously to be low-protein macronutrient omnivores. *Scientific Reports* , **12** , 1–9. https://doi.org/10.1038/s41598-022-19742-z

Rode, K. D., Robbins, C. T., Stricker, C. A., Taras, B. D., & Tollefson, T. N. (2021). Energetic and health effects of protein overconsumption constrain dietary adaptation in an apex predator.*Scientific Reports* , **11** , 1–12. https://doi.org/10.1038/s41598-021-94917-8

Rode, K. D., Stricker, C. A., Erlenbach, J. A., Robbins, C. T., Cherry, S. G., Newsome, S. D., Cutting, A., Jensen, S., Stenhouse, G. B., Brooks, M., Hash, A., & Nicassio, N. (2016). Isotopic incorporation and the effects of fasting and dietary lipid content on isotopic discrimination in large carnivorous mammals.*Physiological and Biochemical Zoology* , **89** , 182–197. https://doi.org/10.1086/686490

Roman-Palacios, C., Scholl, J. P., & Wiens, J. J. (2019). Evolution of diet across the animal tree of life. *Evolution Letters* ,**3** , 339–347. https://doi.org/10.1002/evl3.127

Santos, E. G., Svatek, M., Nunes, M. H., Aalto, J., Senior, R. A., Matula, R., Plichta, R., & Maeda, E. E. (2024). Structural changes caused by selective logging undermine the thermal buffering capacity of tropical forests. *Agricultural and Forest Meteorology* , **348** . https://doi.org/10.1016/j.agrformet.2024.109912

Schwartz, C. C., White, G. C., Harris, R. B., Cherry, S., Keating, K. A., Moody, D., & Servheen, C. (2010). Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* ,**161** , 1–8. https://doi.org/https://doi.org/10.2193/0084-0173(2006)161[1:TSAEIO]2.0.CO;2

Selas, V. (2000). Population dynamics of capercaillie*Tetrao urogallus* in relation to bilberry *Vaccinium myrtillus* production in southern Norway. *Wildlife Biology* ,**6** , 1–11. https://doi.org/10.2981/wlb.2000.032

Semmens, B. X., Ward, E. J., Moore, J. W., & Darimont, C. T. (2009). Quantifying inter- and intra-population niche variability using hierarchical Bayesian stable isotope mixing models. *PLoS ONE* , **4** , e6187. https://doi.org/10.1371/journal.pone.0006187

Sergiel, A., Cattet, M. R. L., Kapronczai, L., Janz, D. M., Selva, N., Barton, K. A., Swenson, J. E., & Zedrosser, A. (2020). Do follicles matter? Testing the effect of follicles on hair cortisol levels. *Conservation Physiology* , **8** , 1–10. https://doi.org/10.1093/conphys/coaa003

Posted on 22 Nov 2024 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.173226964.47195579/v1 — This is a preprint and has not been peer-reviewed. Data may be preliminary.

Sergiel, A., Hobson, K. A., Janz, D. M., Cattet, M. R. L., Selva, N., Kapronczai, L., Gryba, C., & Zedrosser, A. (2017). Compatibility of preparatory procedures for the analysis of cortisol concentrations and stable isotope (δ ^{13}C,δ ^{15}N) ratios: A test on brown bear hair. *Conservation Physiology* , **5** . https://doi.org/10.1093/conphys/cox021

Singh, N. J., Danell, K., Edenius, L., & Ericsson, G. (2014). Tackling the motivation to monitor: Success and sustainability of a participatory monitoring program. *Ecology and Society* ,**19** , art7. https://doi.org/10.5751/ES-06665-190407

Stenset, N. E., Lutnæs, P. N., Bjarnadóttir, V., Dahle, B., Fossum, K. H., Jigsved, P., Johansen, T., Neumann, W., Opseth, O., Rønning, O., Steyaert, S. M. J. G., Zedrosser, A., Brunberg, S., & Swenson, J. E. (2016). Seasonal and annual variation in the diet of brown bears *Ursus arctos* in the boreal forest of southcentral Sweden. *Wildlife Biology* , **22** , 107–116. https://doi.org/10.2981/wlb.00194

Stern, J. H., Laidre, K. L., Born, E. W., Wiig, Ø., & McKinney, M. A. (2024). Space-use strategies drive diet composition of Baffin Bay polar bears. *Ecosphere* , **15** . https://doi.org/10.1002/ecs2.4826

Steyaert, S. M. J. G., Reusch, C., Brunberg, S., Swenson, J. E., Hacklander, K., & Zedrosser, A. (2013). Infanticide as a male reproductive strategy has a nutritive risk effect in brown bears. *Biology Letters* , **9** , 20130624. https://doi.org/10.1098/rsbl.2013.0624

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ* ,**6** , e5096. https://doi.org/10.7717/peerj.5096

Stock, B. C., & Semmens, B. X. (2013). MixSIAR GUI User Manual. Version 3.1, March, 1–42. https://doi.org/10.5281/zenodo.47719.1

Stoner, D. C., Sexton, J. O., Choate, D. M., Nagol, J., Bernales, H. H., Sims, S. A., Ironside, K. E., Longshore, K. M., & Edwards, T. C. (2018). Climatically driven changes in primary production propagate through trophic levels. *Global Change Biology* ,**24** , 4453–4463. https://doi.org/10.1111/gcb.14364

Swenson, J. E., Dahle, B., Busk, H., Opseth, O., Johansen, T., Soderberg, A., Wallin, K., & Cederlund, G. (2007). Predation on moose calves by European brown bears. *The Journal of Wildlife Management* , **71** , 1993–1997. https://doi.org/10.2193/2006-308

Thompson, R. M., Hemberg, M., Starzomski, B. M., & Shurin, J. B. (2007). Trophic levels and trophic tangles: The prevalence of omnivory in real food webs. *Ecology* , **88** , 612–617. https://doi.org/10.1890/05-1454

Welch, C. A., Keay, J., Kendall, K. C., & Robbins, C. T. (1997). Constraints on frugivory by bears. *Ecology* , **78** , 1105–1119. https://doi.org/10.1890/0012-9658(1997)078[1105:COFBB]2.0.CO;2

Yoshimura, H., Hirata, S., & Kinoshita, K. (2021). Plant-eating carnivores: Multispecies analysis on factors influencing the frequency of plant occurrence in obligate carnivores. *Ecology and Evolution* , **11** , 10968–10983. https://doi.org/10.1002/ece3.7885

6 | TABLES AND FIGURES

Table 1. Model results from linear regression modelling explaining variation in δ ^{13}C values in brown bear hair from south-central Sweden 1995-2020 (n = 669). We tested for linear patterns as well as log-linear (ln) relationships between response and explanatory variables. We also tested whether stable isotope values responded to food availability in the same year hair was grown, or to food availability in the year prior, i.e., with a 1-year time lag; (lagged), bur the time lag was no supported in δ ^{13}C values (Table S2). Explanatory variables included an annual index of bilberry production (Bilberry), annual number of moose (*Alces alces*) calves produced based on hunter observations after accounting for observation effort (Calf), the annual number of moose harvested, and bear age and sex. We used the difference in AIC$_c$ scores (ΔAIC$_c$) and

model weights (w_i) to determine the most parsimonious model. Beta estimates ($\widehat{\beta}$) and 95% confidence intervals (LCI, UCI) are provided for each explanatory variable in competitive models.

Model	K	ΔAIC_c	w_i	parameter	$\widehat{\beta}$	SE	LCI	UCI
$Calf + ln(Bilberry)$	3	0	1.00					
				intercept	-0.19	0.19	-0.57	0.18
				ln(bilberry)	-0.21	0.05	-0.30	-0.12
				calves	-0.25	0.05	-0.35	-0.14
Calf	2	14.1	0.00					
$ln(Bilberry)$	2	15.1	0.00					
Intercept	1	22.1	0.00					

Model	K	ΔAIC_c	w_i	parameter	$\widehat{\beta}$	LCI	UCI
$Age *\ sex + Bilberry_{\text{(lagged)}}$	5	0	0.90				
				intercept	-0.47	-0.84	-0.10
				age	0.14	0.02	0.26
				sex (m)	1.21	0.61	1.81
				bilberry (lagged)	-0.18	-0.24	-0.12
				age*male	0.57	0.38	0.75
$Age *\ sex + Bilberry_{\text{(lagged)}} + Moose\ Harvest_{\text{(lagged)}}$	6	4.3	0.10				
				intercept	-0.46	-0.81	-0.10
				age	0.14	0.02	0.26
				sex (m)	1.19	0.61	1.77
				bilberry (lagged)	-0.17	-0.23	-0.11
				moose harvest (lagged)	-0.06	-0.14	0.02
				age*male	0.55	0.37	0.74
Bilberr$y_{\text{(lagged)}}$	2	79.2	0				
Moose Harves$t_{\text{(lagged)}}$	2	97.2	0				
Intercept	1	100.8	0				

Posted on 22 Nov 2024 — The copyright holder is the author/funder. All rights reserved. No reuse without permission. — https://doi.org/10.22541/au.173226964.47195579/v1 — This is a preprint and has not been peer-reviewed. Data may be preliminary.